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ANGIOSPERMS¹

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(WITH PLATES I-VII AND FOUR FIGURES)

The general significance of the herbaceous type seems to have first been clearly realized in the classification of plants put forward by CLUSIUS in the seventeenth century. This author divided plants into large groups based on their habit, much in the same manner that the earlier zoological classifications summarized animals under such groups as flying, creeping, swimming, etc. The idea, however, has long been abandoned that the habit of life can serve as a satisfactory basis for either systematic or phylogenetic classification. This consideration does not in any way eliminate the herbaceous type as a physiological assemblage of the greatest importance in the present epoch of the history of the earth. In this connection the question arises as to the origin of a physiological group which is of such high significance. The older view implicitly, if not in actual statement, assumed for the herbaceous type a position of primitiveness. This attitude is well illustrated by such classics as GRAY'S *Structural Botany* and SACHS'S *Lehrbuch*. In these works the woody stem is represented diagrammatically as originating from the linking up of originally

¹ Contribution from the Laboratories of Plant Morphology of Harvard University.

separate fibrovascular bundles by a so-called interfascicular cambium. The parts of the woody cylinder corresponding to the supposed primitive bundles are known in this connection as fascicular wood, and the sometimes depressed segments which intervene as interfascicular wood. When the sunken segments occur (comparatively rarely, and not widely enough distributed to warrant a hypothesis of the origin of the woody stem in general), the old view regarded their sunken topography as resulting from their later origin through the activity of the belated so-called interfascicular cambium. As has been shown by previous reports from this laboratory, the depression of segments of the stem in trees, vines, and woody herbs is a question of growth mechanics and has nothing to do with belated cambial activity. It is intimately connected, in fact, with the appearance of approximated pairs of large rays, resulting from a process of aggregation of the smaller rays of the general wood in proximity to the entering leaf traces. The large rays undoubtedly make their appearance to supply the greater storage necessities, which are a special feature of the more efficient representatives of the dicotyledonous Angiosperms. In other words, the large rays so universally characteristic of the thicker and more woody regions of herbs, whether aerial or terrestrial, are clearly a physiological response to the climatic conditions of modern times in cooler latitudes and higher altitudes, where storage either in stem or seeds becomes of paramount importance.

Since it obviously can no longer be maintained that the woody stem is derived from the apparently simpler herbaceous axis, the question naturally arises whether the reverse relation of origin exists between the two types. To those possessing a knowledge of the past of the great groups of vascular plants this possibility presents no difficulties whatever, since it is certainly known that many of the herbaceous living representatives of cryptogamic groups have had as ancestors forms of strikingly arboreal habit. This situation indeed provoked a long continued contest as to whether the treelike Cryptogams of the paleozoic periods were not in reality seed plants, as are arboreal types with secondary growth at the present day. It has been emphasized

by one of us (4), however, that the herbaceous Cryptogams are distinctly the result of degenerative changes in the older and ancestral forms. The herbaceous type in the Angiosperms, as will be pointed out in the sequel, has had an entirely different mode of origin from that illustrated by many existing herbaceous Cryptogams.

Nearly a decade ago EAMES (2), in a publication from this laboratory, made a comparative study of the herbaceous type, which was particularly focussed on the Rosaceae, since this group presents in relative abundance closely related forms of woody and herbaceous texture. This investigator concluded that there is clear evidence in the Rosaceae for the origin of herbaceous stems from woody, as a consequence of the formation of large storage rays in relation to the incoming foliar traces. These rays usually extend some distance below the foliar trace, and also may be developed above it. In the horizontal aspect of the axis, in the region of the node of stems with a well developed fibrovascular cylinder, the storage parenchyma related to the leaf traces can be seen subtending them externally. The development of these masses of storage tissues in woody stems and in correlation to the vascular supply of the leaves (since the masses in question not only subtend the foliar traces vertically but, in cylinders of any thickness, likewise in the radial dimension as well) automatically results in the transformation of the continuous dicotyledonous woody cylinder (ultimately at any rate) into a circular series of discontinuous fibrovascular segments, the fibrovascular bundles so characteristic of herbaceous stems. Accompanying the development of the large foliar rays, as pointed out by EAMES, is the final degeneracy of the rays of moderate size, which are normally characteristic of the woody cylinder of arboreal Angiosperms.

In an article published a few years later, SINNOTT and BAILEY (5) attack EAMES'S conclusions, and while admitting the derivation of herbaceous forms from arboreal or woody, they question the existence of foliar rays subtending the foliar traces vertically and horizontally. They admit the frequent presence of foliar rays in the subterranean stem of herbs, but deny that this has any bearing on the question of the origin of the herbaceous type. They

consider that the presence of foliar rays in aerial stems is rare, and that this supposed absence constitutes a weak point of the hypothesis of the derivation of the herbaceous type, which they ascribe to the senior author of the present article. In a recent article WHITAKER (4) has demonstrated clearly the insecure basis of the assertion of SINNOTT and BAILEY as to the absence of foliar rays in the aerial axis of the Compositae, perhaps the most important and certainly the most easily available group which is represented in temperate climates by typical herbs. One of us (4) has likewise recently discussed the anatomy of the flowering leafy stem of *Helianthus*, with similar conclusions.

It will serve a useful purpose to begin the description of the herbaceous stem, from the aspects included in the present discussion, with a description of the aerial stem in certain common Compositae. Fig. 1 shows a transverse section of the stem of *Aster novae-angliae*, common in the eastern states. The lower region of the axis above ground is represented. To the left at the top of the figure can be seen a marked depression of the surface of the stem. This corresponds to the median foliar ray of a leaf attached to the stem slightly above the plane of section. This ray is characterized not only by the depression it causes on the periphery of the stem, but also by the absence of vessels in its external region. Below this ray and on the left occurs another foliar ray, corresponding to one of the two lateral traces of the leaf under consideration. This ray is substantially like the one subtending the median trace, but is smaller in size and causes a less marked depression on the surface of the woody cylinder and on the periphery. The foliar ray of the right-hand lateral trace is about as far to the right of the median ray as the left ray is on the opposite side. It will be noted that the depression in this case is very slight, and that the foliar ray is deeper radially and less broad than the other two similar structures. Since the traces do not always penetrate the stem at the same level, the rays which correspond to the three traces of the same leaf usually do not present the same appearance in details in a given section. An examination of the rest of the woody cylinder in fig. 1 shows that no foliar rays closely resembling the three under discussion can be distinguished. This results from the fact that

the foliar rays of the species of *Aster* under consideration extend only a slight distance downward in their normal form, and as a consequence in the lower and stouter region of the part of the stem above ground usually only three typical leaf rays can be seen in a given plane of section.

Fig. 2 shows a transverse view of the same *Aster* in the upper region of the aerial stem. Here the woody cylinder appears much thinner, in spite of the fact that the magnification is considerably higher than in fig. 1. A projection on the upper surface marks the position of the median trace of a leaf belonging to the nodal region from which the section has been made. The higher part of the stem, as is often the case in above ground herbaceous axes, shows the leaf traces and their corresponding foliar rays as projections from the surface of the woody cylinder, and not depressed, as is the normal condition for these structures in herbs of woody texture or in the woody lower region of the aerial stem of more typically herbaceous axes. In addition to the three projecting leaf traces and their corresponding foliar rays, which occupy adjacent positions on the upper surface of the woody cylinder in fig. 2, are to be seen 5 or 6 less prominent traces and corresponding foliar rays belonging to leaves higher up on the stem. In figs. 3-5 is reproduced the whole of the woody cylinder of fig. 2, on a somewhat higher scale of magnification. It will be seen from figs. 2-5 that there are 8 leaf traces clearly obvious, alternating with as many "common" or "cauline" segments. This interesting situation results from the fact that in the upper more herbaceous region of the stem the foliar rays extend, as such, much deeper down than in the case of the lower woody region of the same aerial axis. Consequently a number of leaf rays corresponding to the traces of leaves at several nodes can be distinguished in a single transverse section through the higher region of the stem. SINNOTT and BAILEY (5) have denied the possibility of the conditions represented in figs. 2-5. The topography in question is in fact extremely common in herbs of a certain degree of advance from the woody primitive ancestral forms. Naturally it does not occur in extremely woody herbs, on the one hand, because in these very few foliar rays can usually be seen at one time, and these in rather close vertical

proximity to the next superior node. In extremely slender herbaceous stems, on the other hand, by the thinning of the woody cylinder, the foliar ray radially external to the leaf trace is eliminated, and only the flanking portions of the ray on either side of the foliar trace in its upward vertical course in the stem can be distinguished. It follows that an alternation of foliar rays and stem bundles is extremely common in herbs which are transitional in their texture, but naturally does not occur in either extremely woody herbs or in those which are strikingly herbaceous.

In fig. 6 is shown the foliar ray and its inwardly subtending leaf trace. The foliar trace may be recognized as radially disposed groups of vessels separated by equally radial bands of parenchyma. Externally the vessels give place to fibers and parenchyma, which constitute the external or confronting portion of the foliar ray. Lateral to the vascular leaf trace on either side can be distinguished the flanking portions of the foliar ray. It follows that a foliar ray may consist of parts flanking the leaf trace and separating it from the adjacent stem segments, as well as a region subtending the foliar strand externally. In thinner stems the latter portion progressively disappears, until only the flanking portions of the ray persist. This situation has recently been represented in diagram by WHITAKER. SINNOTT and BAILEY (6) have, however, quite failed to understand the situation. Since the genus *Aster* is a somewhat woody herb the topography represented in figs. 2-5 is usual in the upper region of the stem of various species.

We may now pass to a more herbaceous illustration of the Compositae, namely *Helianthus*, which has already been used (4) to exemplify the anatomical conditions in regard to the topography of the foliar rays. Corresponding to its less woody structure is the fact that foliar rays possessing depth enough to subtend as well as flank the leaf trace are confined usually to the lower portions of the aerial stem. In the superior portion of the latter the leaf rays are purely flanking in their development, on account of the slender nature of the woody cylinder. Disregarding the latter condition for the moment, we may turn our attention to the lower region of the subaerial stem. Fig. 7 is a foliar ray from the base of the stem of *Helianthus annuus*. Obviously the continuity of the woody cylinder is broken by a strongly developed radial band

of storage parenchyma, the foliar ray subtending the leaf trace in its vertical course in the stem. Along the inner margin of the ray may be seen the elements constituting the foliar trace. Fig. 8 represents the foliar ray of *Helianthus orgyalis*, a perennial and somewhat more woody species than *H. annuus*. This is in accordance with a general principle, for, other things being equal, the more woody an herb is, the longer radial and the less tangential and vertical extension have its foliar rays. Conversely, the more herbaceous the texture, the shorter the radial extension of the leaf rays and the greater their vertical length. Another feature of contrast can be distinguished between the rays shown in figs. 7 and 8. In the former the ray is quite homogeneous in structure, while in the latter narrower fibrous elements constitute radial bands in the substance of the ray. This contrast is a common one between the foliar rays of woody and more advanced herbs.

We may now turn to the relative size of the foliar traces and rays in more and less herbaceous forms, as well as the contrasts in the structure of the rays presented in these various modifications of the herbaceous type. The best way to make these important features clear is to choose corresponding regions of the stem, progressively more herbaceous in their texture, from different species of the same genus. Fig. 10 shows the vertical tangential view of a foliar ray from the lowest region of the aerial stem of the somewhat woody *Helianthus hirsutus*. It will be observed that the structure of the foliar ray in this instance is far from homogeneous, since bands of fibers are common in its substance, and with them vessels likewise occur. In this instance the foliar ray is obviously in the process of organization from the ordinary wood, namely, from smaller rays, separated by strands of vessels and fibers. In more advanced herbs belonging to *Helianthus*, as will shortly appear, the fibers and vessels progressively disappear, until the final result is a large mass of radial and longitudinal storage tissue, the typical foliar ray.

Fig. 10 represents the foliar ray in a condition of aggregation from smaller rays. SINNOTT and BAILEY (6) have denied the possibility of the appearance of foliar rays as the result of aggregation. Their error in this respect has been pointed out recently by HOAR (3), and consequently need not be referred to further here.

In one of the uppermost members of the aggregation (fig. 10) may be seen a darker dot, representing the transverse section of the outgoing foliar trace. The trace is obviously extremely small in size. Fig. 14 illustrates a portion of fig. 10 under a higher degree of magnification. The composite character of the foliar ray is now more easily seen, for rays, fibers, and vessels are all evident as component parts of the aggregate foliar ray. Fig. 11 is a tangential view of the foliar ray of *H. tuberosus*, on the same scale of magnification as fig. 10, representing a similar aspect of the ray in *H. hirsutus*. The contrasts between the two figures are both interesting and important from the standpoint of the question of the origin of the herbaceous type. The leaf ray in fig. 11 is much more clearly developed than in fig. 10. The fibers are much reduced in quantity and very few vessels are to be seen. Another important contrast is presented both by the size of the foliar ray and of the foliar trace to which it is related. The leaf strand appears as a dark, somewhat triangular spot in the upper part of the ray, as shown in fig. 11. In fig. 9 is shown a portion of the ray of *H. tuberosus*, under somewhat higher magnification than fig. 11. By comparing figs. 9 and 14, which represent details of the foliar rays of *H. tuberosus* and *H. hirsutus* under the same degree of magnification, it is clear that the ray in the former and more herbaceous species is much larger, and also contains more parenchymatous storage tissue than in the latter and more woody species.

The greatest contrast in every detail of organization, as well as in relative size, however, is presented by *H. annuus*, the most herbaceous of the three compared species. In fig. 12 is shown the tangential view of the leaf ray of this sunflower, under the same magnification as in figs. 10 and 11. The huge size of the ray is clearly seen. Not less striking is its homogeneous organization, resulting from the virtual disappearance of the fibers and vessels, which betray the aggregated character of the rays in *H. hirsutus* and *H. tuberosus*. The foliar ray in *H. annuus* is of the type which we have called compound, since with a homogeneous structure it still betrays evidence (from the comparative anatomical standpoint) of having been organized by the fusion of a number of ordinary wood rays in the vicinity of the foliar trace, with the

concurrent transformation of their separating fibers and vessels into storage elements. This results in the final formation of a large homogeneous complex of radial storage tissue, intimately connected both topographically and physiologically with the leaf trace. Fig. 12 shows also the leaf trace enlarged to the same proportionate size as the huge storage ray to which it belongs.

It is clear from the comparison of the foliar rays in the species of sunflower that the size of the ray, the size of the leaf trace, and the degree of parenchymatous homogeneity of the foliar ray, all directly correspond to the degree of herbaceous development of the species. *Helianthus annuus*, which is not only the most herbaceous of the three, but is of such vigor as to be able to proceed from seed to seed in a single season, is characterized by marked superiority in all three particulars. Fig. 13, showing the structure of the leaf ray of *H. annuus* under the same enhanced magnification as the other two species in figs. 9 and 14, makes it clear that the structure of the foliar ray in the former species is characterized by enough variety in the dimensions of its constituent elements to reveal its composite derivation from the modification of wood rays, fibers, and vessels.

Having made a comparative study of the foliar ray in progressively more herbaceous species of *Helianthus* in the lower region of the aerial stem, attention may be given now to the considerations represented in the upper nodes of the axis. Fig. 15 illustrates the outstanding leaf trace of an upper node of the stem of *H. tuberosus*. It is separated from the stem bundles on either side by flanking parenchymatous bands of the foliar ray. The large radial extension of the foliar ray which marks its organization in the lowest part of the stem has become progressively reduced in the region of higher nodes, until at the level of fig. 15 it has entirely disappeared. This simple geometrical condition has been diagrammed recently by WHITAKER (7) and need not be further considered here.

Another feature of interest, which is particularly obvious in the upper nodes, is the condition of cambial activity in the foliar and cauline bundles respectively. Fig. 16 represents the stem or "common" bundle immediately to the right of the foliar trace in fig. 15. Above is to be seen the fibrous pericycle of the bundle

protecting the phloem. Separating the phloem from the xylem is a well marked cambial region, characterized by the regularly seriate arrangement of its cells. Fig. 17 represents the foliar trace of fig. 15, under the same magnification as fig. 16. It is clear that the cambial activity found in the stem bundle is conspicuous by its absence in the leaf trace, since there are no regularly radially arranged cells intervening between xylem and phloem.

Before discussing the significance from the evolutionary standpoint of the facts elucidated in figs. 15-17, it will be well to consider the conditions present in the bundles of the root, using *Aster*, since this genus presents a more illuminating range of organization in the root than that which characterizes *Helianthus*. Fig. 18 represents a transverse section of the mature root of *Aster Shortii*. Root hairs are conspicuous by their absence, and the strong development of the secondary wood is very obvious. In the midst of the secondary organization of the wood can be seen a small 5-angled star of primary xylem, the points of which alternate with the 5 dark hued masses of phloem seen on the margin of the fibrovascular cylinder of the root. Fig. 19 is a transverse section of a young root of the same species of *Aster*, in which the secondary growth of the xylem is just beginning. The primary xylem star with its 5 points alternating with 5 angles of phloem can distinctly be seen. Root hairs are present on the surface of the root, but are beginning to disappear, as is normally the case in roots in which secondary structures have begun to form. Fig. 20 represents a very different type of root, in which the organs are distinguished by the indefinite persistence of the root hairs. This condition is well shown by the varieties of the somewhat inconstant species *Aster umbellatus*. Here the roots continue as hirsute structures for several years, and in fact this condition persists until they have become quite dark with age and have begun to decay. Fig. 20, which represents an old root of this species, shows that the persistence of the root hairs is paralleled by the absence of secondary structures in the cylinder of the organ. This is an interesting general condition of the organization of permanently hairy, and, as a consequence, presumably persistently absorbent roots.

Fig. 21 shows the very herbaceous stem of *Aster tataricus*, which differs from the American species in the strikingly soft texture and great vigor and thickness of its stem. This condition is shown in the transverse section by the large pith surrounded by a series of a distinctly separated and slender fibrovascular bundles. Another distinguishing feature is the large number of foliar traces which proceed from each leaf, these being as many as 7 (as may be seen in the upper region of the figure) in contrast with the 3 which mark the numerous woody species of *Aster*. It is clear, therefore, that *A. tataricus* is a particularly well developed herb, and in this respect presents a marked contrast with the predominantly woody herbaceous species of *Aster*. The roots of *A. tataricus* are like those of *A. umbellatus* in that they are permanently without development of the secondary wood, and likewise have persistent root hairs, albeit these are much more delicate than in the latter species.

Bringing together these results, we conclude that in woody species of *Aster* persistent root hairs and absence of secondary wood are correlated features of the organization of the root. In roots with evanescent root hairs the disappearance of these marks the beginning of the secondary activities in the wood. In *Aster tataricus*, which is remarkably herbaceous in its general habit in contrast with the species of the genus as a whole, a similar correlation is found between the persistence of root hairs and the absence of secondary growth. This will not be discussed further at the present time, but it will elsewhere be shown that there is a general correlation between a high absorptive capacity of the root (associated morphologically with persistent root hairs) and the absence of secondary woody developments in the central cylinder of the root. In other words, the herbaceous habit in roots is marked both by high absorptive efficiency and by the absence of secondary woody growth.

In the light of these preliminary results in the case of the root, the situation already described for the leaf traces of *Helianthus* becomes particularly significant. A general examination of the species of this genus, particularly of those presenting in a more marked degree the herbaceous habit, indicates that cambial activity

is very generally absent in the strands which conduct the assimilates from the leaf into the stem. The conducting efficiency of the foliar trace would obviously be considerably reduced were part of the assimilates to be used in the growth of the bundles of the foliar traces instead of being transferred intact to storage in the stem or seeds. High conductive efficiency, notably correlated in herbs with the assimilative productiveness of the leaf, as will be pointed out later, is in general associated with the loss of cambial activity in the foliar traces as they enter the cylinder of the stem. In the root the most obvious interpretation of the absence of secondary woody growth is the unfavorable effect that a jacket of secondary elements would have on the ease of penetration of the water absorbed by the root hairs into the water-conducting tissues of the central cylinder. Since the essential conditions of the loss of a cambium are different in stem and root, it is clear that both may not present the feature of the loss of secondary activities in their fibrovascular structures at the same time. In other words, the stem may be herbaceous and the root woody; or vice versa, the stem may be woody and the root herbaceous. The former condition is well exemplified by certain species of *Papaver*, while *Aster* furnishes examples of the latter.

We may now turn to a type which is still more delicate in its herbaceous texture than are either *Aster* or *Helianthus*. Like the sunflower, the buttercup often serves as an example of the herbaceous type in laboratory exercises, and for that reason it is chosen in this connection, as illustrating a common and easily obtained plant. Fig. 22 illustrates the organization of a small stem of *Ranunculus acris* in the region of the branching node. The larger cylinder below represents that of the main axis, while the branch cylinder is smaller and appears above. Inclosing the branch and fused with it is the base of a leaf, in which may be distinguished 5 fibrovascular bundles, the leaf traces. As the cylinders of axis and branch come together, the phloem of their uppermost and lowest bundles respectively face one another. In fig. 23 is shown a somewhat lower plane of section in a rather larger stem than that illustrated in fig. 22. Here the union of secondary and main axes has taken place with interesting results. In the

outer region of the pith corresponding to the medulla of the secondary axis are several amphivasal concentric fibrovascular bundles, precisely similar to those so commonly found in the stem of monocotyledons. The amphivasal strands are the result of the fusion of the confronting bundles of main axis and lateral branch by their phloems. This condition is not an uncommon one for dicotyledonous stems of marked herbaceous nature, particularly when they bear large leaves with many foliar traces entering the axis at the nodes. Other examples of this feature will be supplied later.

Fig. 24 shows a section of the stem of a buttercup at some distance below the node. A rather old stem has purposely been chosen, so that the identity of the foliar traces in the stem may readily be distinguished. In such stems, in the later summer, gummosis invades the cavities of the vessels of the foliar traces, a feature which makes the leaf traces stand out even in low magnifications. To the extreme right is seen the median trace of the leaf, and above and below on either hand are the lateral traces, two on either side. The foliar traces are emphasized by their blackness, resulting from the mucilaginous contents of their vessels. Fig. 25 is a portion of a section similar to that illustrated in fig. 24, somewhat more highly magnified. It is now quite easy to discern that the two outside bundles have vessels plugged with darkened contents, while the vascular structures in the central bundles appear quite clear and devoid of gummosis. Fig. 26 furnishes a further example of the phenomenon of gummosis in the external bundles, which here as in the other instances are foliar traces. The leaf trace to the right is much smaller than its counterpart on the left, and represents in fact an extreme lateral trace of the leaf.

In fig. 27 appears a part of a stem preserved in the early summer, in which as a consequence gummosis is not present in the vessels of the foliar traces. The magnification is greater than in the two preceding figures, and more details of the structure of the fibrovascular bundles are evident. Obviously the two larger bundles at the ends present a different structure from those toward the center. This expresses itself in a more parenchymatous organization of the xylem, in which comparatively few vessels are distributed

in a large amount of heavily pitted wood parenchyma. In the cauline strands, on the contrary, the xylem is more vascular and the parenchymatous elements are less abundant and thinner-walled. A further distinction is the absence of cambial activity in the foliar traces, a situation which leads to a less regular arrangement of the cells than is found in the central strands. In fig. 29 appears another illustration on a somewhat higher scale of magnification than that in fig. 27. The bundle to the right, which is a cauline strand, shows distinct evidence of cambial activity such as is figured in STRASBURGER'S *Botanische Practicum*. On the other hand, the foliar strand, which here lies to the left, is without cambial activity, as indicated by radial regularity. Fig. 31 is a partial view of another transverse section, in which a large cauline bundle lies on the left, while on the right is another foliar bundle, in this case also distinguished by the absence of cambial activity. To make clear that cambial activity is really absent in the foliar strands of the buttercup in the upper part of their course in the cylinder of the axis, several figures under considerable magnification have been introduced. Fig. 28 shows a foliar strand under a moderately high magnification. It is clear that cambial activity is absent here, since there are no regularly radially arranged rows of cells intervening between xylem and phloem as is the case with the stem bundles. Moreover, the less woody organization of the xylem is a further consequence of this absence of cambial increments. Fig. 30 shows another foliar bundle in the stem under somewhat higher magnification. The absence of cambial growth is here still clearer. Fig. 32 shows a still more enlarged view of one of the leaf traces in the stem, and the absence of any evidence of secondary activity is apparent.

It is obvious that in the buttercup, precisely as in the sunflower and to a less degree in the aster, there is a distinct and striking intermission of cambial activity in those fibrovascular strands in the stem which have entered from the leaves. In the case of *Aster* attention has been called to the absence of secondary additions of the xylem in the case of species in which the root hairs are indefinitely persistent. The root of the buttercup, as has long been known, is without secondary accretions to the wood. Fig. 33

shows the root of *Ranunculus acris*. The absence of secondary activities is striking. Sections through the subterranean perennial stem of the buttercup show leaf traces and root bundles in the axial region, both contrasting with the bundles of the stem proper by the entire absence of cambial activity. It is clear that in the buttercup the herbaceous habit has completely taken possession of both stem and root, so that secondary activities are equally conspicuous by their absence, both in strands destined to the leaves and to the roots. Even in the perennial and often rather thickened subterranean stem of *R. acris*, the fibrovascular tissues do not ordinarily show themselves so well developed as to manifest the presence of typical foliar rays subtending the foliar traces. One can easily find such rays in the perennial subterranean stem of *Thalictrum*, however, and also in the aerial stem of various woody species of *Clematis*. It is obvious that typical foliar rays associated with distinctly woody perennial stems lie in the phylogenetic past of extremely herbaceous representatives of the Ranunculaceae, precisely as they do in the case of the more woody herbaceous types which ordinarily and likewise represent the Compositae in temperate climates.

We may now pass to other illustrations of the herbaceous type as characterized by delicate stems and numerous leaf traces entering the stem at the node. The Umbelliferae will serve as our first illustration in this connection. Fig. 34 is a total transverse section of a node in the aerial axis of a species of *Sanicula*. Uppermost and toward the right is a leaf base in the act of fusing with the stem. It shows the presence of a considerable number of foliar traces, which become still more numerous a little lower down by subdivisions of the original strands. Axillary to the foliar base is the cylinder of a lateral branch. This spreads out laterally over the surface of the main cylinder, in such a manner that the bundles of the branch present themselves to those of the main axis by their phloems. Fusion of these mutually confronting strands takes place in such a manner that a number of amphivasal strands results. The formation of these begins in the axillary region and proceeds progressively downward on either side. In fig. 35 appears a section somewhat lower down on the same axis as that shown

in fig. 34. The foliar traces are more numerous at this level, and are beginning to draw in toward the fibrovascular cylinder of the main axis. It will be seen that the bundles of the axis are amphivasal in the upper middle region. On the left is one of the bundles of the branch pursuing a tangential course to become fused with the face of the more lateral bundles of the cylinder of the main axis. The bundles of the main stem become amphivasal for nearly two-thirds of the perimeter of the cylinder before the union of the branch with the parent axis is completed. One of the amphivasal strands from the median upper region of fusion is shown in fig. 36. It is clear that the organization is quite similar to that of the Monocotyledons, the only contrast being in the presence of secondary growth. This, however, is not a matter of great importance from the evolutionary standpoint, since often in the Monocotyledons secondary activities can be recognized in the nodal region of the stem, as has been pointed out by CHRYSLER (1) and others. It is of interest to observe that in this genus the fusions which result in the formation of amphivasal bundles take place on the outside of the fibrovascular ring and not internally as in the buttercup. This situation seems to be rather a common one for the Umbelliferae as a whole. As the nodal region is passed the amphivasal bundles open up toward the outside of the stem and constitute dense, flat, fibrovascular segments of collateral organization. Similar conditions in regard to the resolution of the amphivasal strands are found in the buttercup.

Fig. 37 illustrates the organization of the stem in the nodal region of *Rumex* sp. The foliar traces are numerous, and to a large extent have passed into the cylinder. The periphery of the medullary region is occupied by a number of fibrovascular bundles of amphivasal organization. These are the result of the fusions of strands of the secondary and main axes by their phloems. The amphivasal strands in lower regions of the internode undergo fusions with the bundles of the cylinder, and finally completely disappear before the next node is reached. Fig. 38 shows a part of fig. 37 more highly magnified. The amphivasal strands can be seen on the medullary side of the collateral bundles which constitute the main cylinder.

These illustrations, which might be indefinitely multiplied from the nodes of herbaceous Dicotyledons, make it clear that amphivasal bundles resembling those of the Monocotyledons are frequently present in the nodal regions of dicotyledonous herbs, and result from the fusion of strands by their phloem faces. The similarity of the conditions in the two great divisions of the Angiosperms may be confirmed by an illustration taken from the grasses. Fig. 39 shows the nodal region of the upper part of the aerial stem of *Zea*. A leaf base is uniting with the stem, and on the upper left the fusion of the foliar vascular supply with that of the axis is farther advanced than it is on the lower right side of the illustration. This condition is due to the fact that either the section is not exactly transverse, or else the fusion of the leaf base is not effected in an exactly horizontal plane. It matters little which explanation be adopted. The bundles which enter the stem from the leaf are obviously extremely numerous, and their accommodation in the stem is accordingly a matter of some complexity. The device by which their reception is effected is by means of fusions similar to but more complicated than those exemplified in the dicotyledonous types figured. Fig. 40 shows a part of the upper left hand portion of fig. 39 more highly magnified. Three amphivasal bundles can be seen forming an oblique line from the lower left to the upper right of the figure. Between these lie other bundles which are in the act of fusing. A characteristic feature of the nodes of the aerial stem of grasses, sedges, and rushes is the presence of amphivasal bundles in the region of the nodes, resulting from the fusions effected in connection with the entry of the numerous foliar bundles into the stem. In the mass of Monocotyledons these amphivasal fusions are no longer found in the often highly specialized, annual, aerial axis, but are confined to the more primitive, perennial, subterranean stem. In the Scitamineae and true palms amphivasal bundles are usually entirely absent.

We may now turn to further illustrations of the absence of cambial activity in foliar strands which have recently entered the stem in the dicotyledonous Angiosperms. The legumes are a very important family of Dicotyledons, which are represented in temperate regions by many herbaceous forms. Fig. 41 shows the

infranodal region of the common garden bean. Since the lower part of the aerial stem is represented, the cylinder is somewhat thick and woody, as well as round in form. A leaf trace occupies the central region of the figure, and it is clearly marked by the absence of the dark cambial zone, which marks the stem bundles on either side. It is evident that absence of secondary activity is a feature of the leaf trace in a form which for many years has served in the laboratory for an example in studying the anatomy of the herbaceous dicotyledonous stem. As a further illustration the aerial axis of the common red clover (*Trifolium pratense*) may be used. Fig. 42 makes clear the conditions found in the nodal region of this species. A well marked black band indicates the cambial activity of the bundles of the stem proper. In the median region appears a leaf trace which is quite conspicuously without cambial activity, and in this respect presents a marked contrast with the cauline bundles which are adjacent to it on either flank. These illustrations, which might be indefinitely multiplied from the common leguminous types, clearly show that in this group the tendency toward the elimination of cambial activity in the leaf trace makes itself obvious.

The garden poppy will supply an example from another and somewhat distant group. In fig. 43 is shown the region of the node in the annual garden poppy of hybrid origin (*Papaver cross*). The foliar traces in many cases in this genus enter the stem as double strands. One of these pairs appears in the center of the figure, and it can easily be seen that its constituent strands are without the secondary activity due to the presence of the cambium, exemplified in the cauline bundles on either side of the foliar pair. Fig. 44 shows a total transverse section of the stem of the wild morning glory (*Convolvulus* sp.). On the upper side of the cylinder is shown a broad arc breaking away from the fibrovascular ring. This is the leaf trace of the leaf attached to the next node above. Nearly opposite, but somewhat obliquely placed, is a trace of a still higher leaf. It is clear that the foliar traces show a considerably less degree of secondary growth than is found in the fibrovascular tissues of the stem proper.

An examination of many nodes in herbaceous Dicotyledons has made it clear that there is a strong tendency for cambial activity to disappear in the leaf traces as they enter the cylinder of the stem. Even when the foliar trace does not intermit its secondary growth, there is always a considerable reduction of activity in this respect. This phenomenon, in fact, is not confined to Dicotyledons, but is also exemplified in Gymnosperms, both living and extinct, and in Cryptogams where secondary woody tissues are developed. There is an obvious advantage to the plant in the elimination or reduction of cambial activity in the foliar strands, since the food materials elaborated in the leaves are thus more certainly assured of transfer, without essential loss, to the storage regions of the stem. In the case of the herbaceous Dicotyledons, however, the much greater degree of assimilative activity causes so great an emphasis of the limitation of cambial activity in the leaf traces that in a large number of cases it disappears altogether. This feature, together with the usual multiplication of leaf traces in the more pronounced herbs, has produced in extreme instances among the Dicotyledons conditions which are not essentially different from those obtaining in the anatomical organization of the Monocotyledons.

In text fig. 1 is shown a stereodiagram of the stem of *Helianthus* in the region of a node. The node chosen is neither from the extremely upper region of the aerial stem, nor from its stout woody base. There are six leaf traces present, three facing, and three on the opposite side of the stem. Each trio of traces belongs to one of the opposite leaves. On the remote side the lateral traces are represented as passing into the leaf base, while the median is still in the axis. The nearer aspect of the stem is deprived of its superficial tissues, so that the relation of the traces to the organization of the wood may easily be seen. In the transverse aspect each leaf trace is clearly subtended and flanked by the storage tissues of the foliar rays. As the leaf rays descend in the stem they fork as a result of the intrusion of a median tongue of wood into the ray from below. Each foliar strand in the not too slender axis of *Helianthus* is accordingly related to a foliar ray which subtends it radially and at the same time accompanies it on either flank.

The accuracy of text fig. 1 may be confirmed by reference to figs. 7-14. It follows from simple geometrical considerations that as the stem becomes more slender in its upper portion, the radially subtending part of the foliar ray in the thicker region of the stem automatically disappears from view.

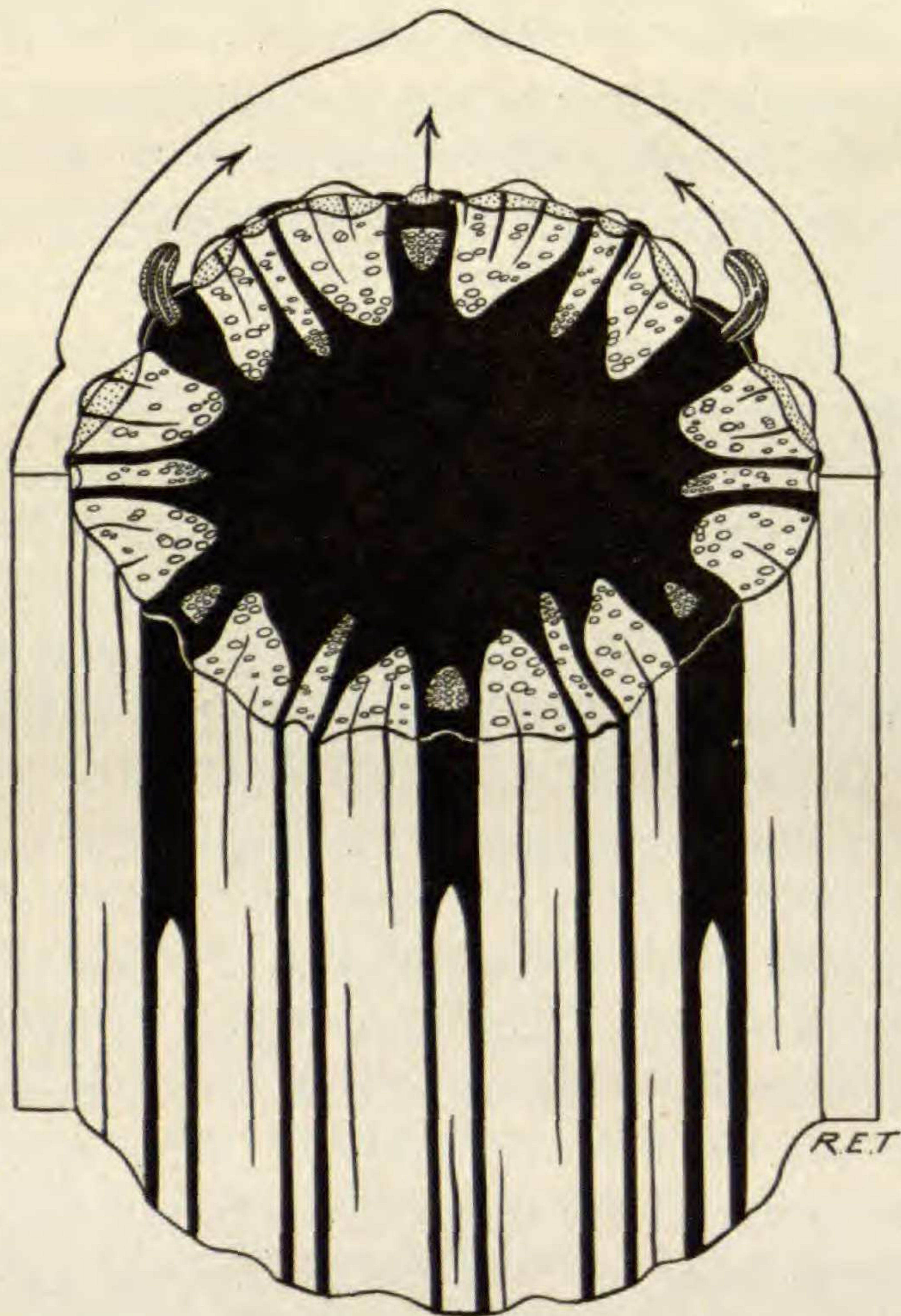
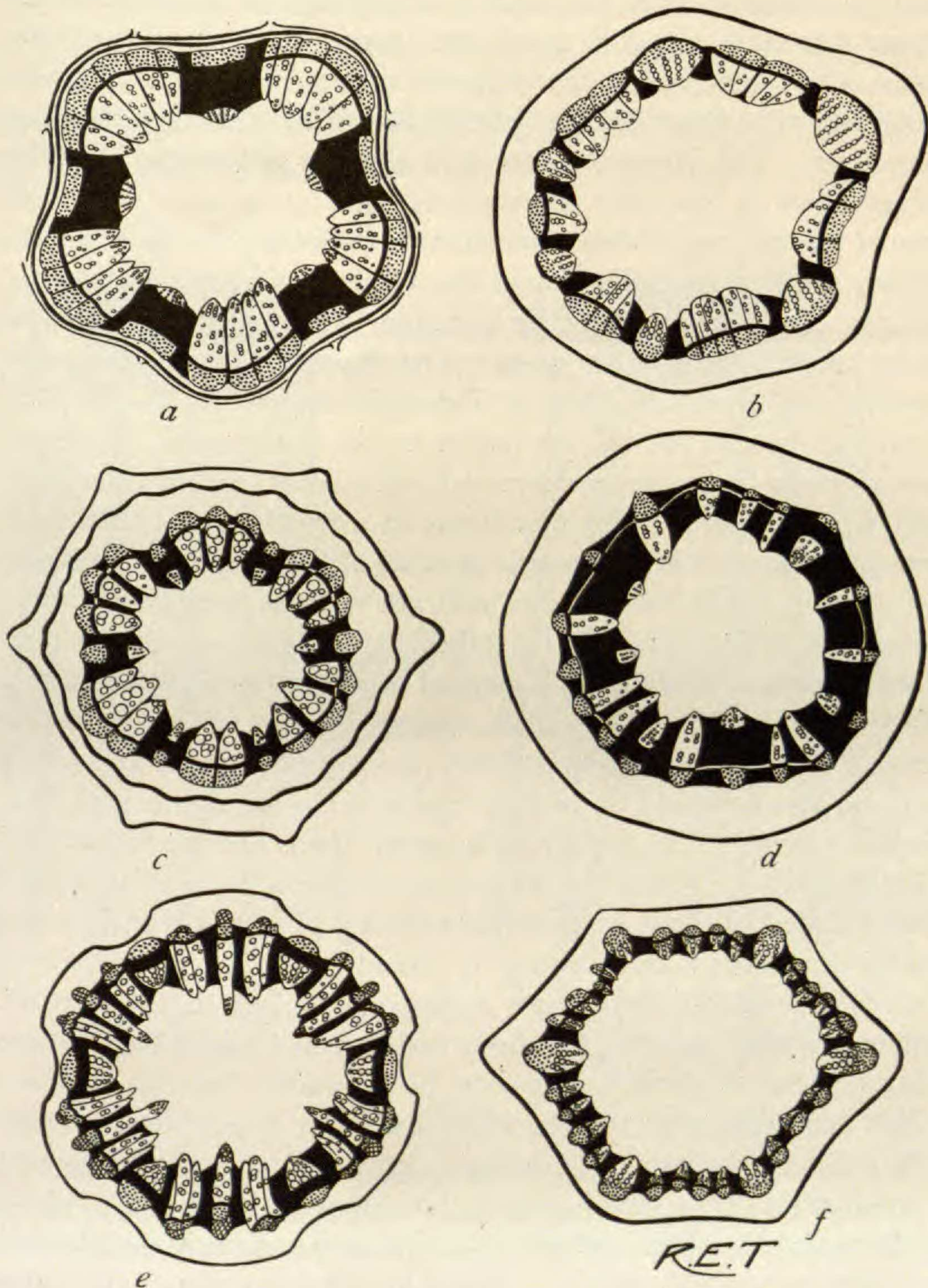


FIG. 1

The cambial conditions in dicotyledonous herbs are illustrated by text fig. 2, in which *a* represents the stouter lower region of the aerial axis of an herbaceous *Potentilla*. There are 5 outstanding segments of the stem, alternating with 5 depressed. The projecting portions of the wood cylinder show the presence of a cambium, indicated by a heavy line separating the xylem and phloem. In the depressed segments the wood has become largely parenchymatous storage tissue, subtended inwardly by the vascular foliar



R.E.T

FIG. 2

traces. There is little or no cambial activity to be observed in these segments. In *b* is shown the upper slender region of the same aerial stem. Here the segments corresponding to leaf traces contrast with those in the former figure by their outstanding character. The absence of cambial activity, however, is to be observed as in the foliar segments of the stouter axis. The leaf traces are also more numerous than in the other instance, a condition not at all uncommon in the upper regions of herbaceous stems. This phenomenon, for example, is found in the common bean, and in many other cases. The depressed segments in the slender portion of the stem of *Potentilla* correspond to the outstanding ones in the thicker region nearer the ground. Cambial activity is indicated in the depressed portions of the stem separating xylem and phloem. The conditions in a woody axis of *Clematis* are shown in *c*. The depressed segments of the cylinder correspond in position to the foliar traces, and are without cambial activity. The outstanding arcs, on the other hand, represent the cauline bundle system, in which well marked secondary growth is present. In *d* is shown the subterranean perennial stem of *Actaea*, as an example of the essential similarity in organization of terrestrial axes to that found in the woody region of the aerial stems of herbaceous types. The broad, black, radial bands are the foliar rays. In proximity to a node the leaf ray is subtended by a broad radial band of storage tissue, and cambial activity, as represented by a line separating xylem and phloem, is absent. In the case of traces which are remote from their corresponding leaf in the vertical plane, cambial activity has been restored and the foliar storage parenchyma is divided into two by a woody central isthmus. This condition may well be compared with that shown in text fig. 1 for *Helianthus*. The topography of a moderately thick and woody node of the aerial stem of *Helianthus* is shown in *e*. The 6 foliar segments of the cylinder are depressed and show the absence of distinct cambial activity. The subtending portion of the foliar ray is only moderately well developed in this instance to correspond to the slight degree of thickening of the stem. In the outstanding portions of the cylinder a cambium is present and is conventionally represented by heavy lines separating xylem and phloem. In *f* is

shown an upper slender region of the stem in the sunflower. In accordance with the general principles formulated in the other examples, the foliar segments are here both outstanding and devoid of cambial activity. The remaining bundles are depressed and show the presence of secondary growth.

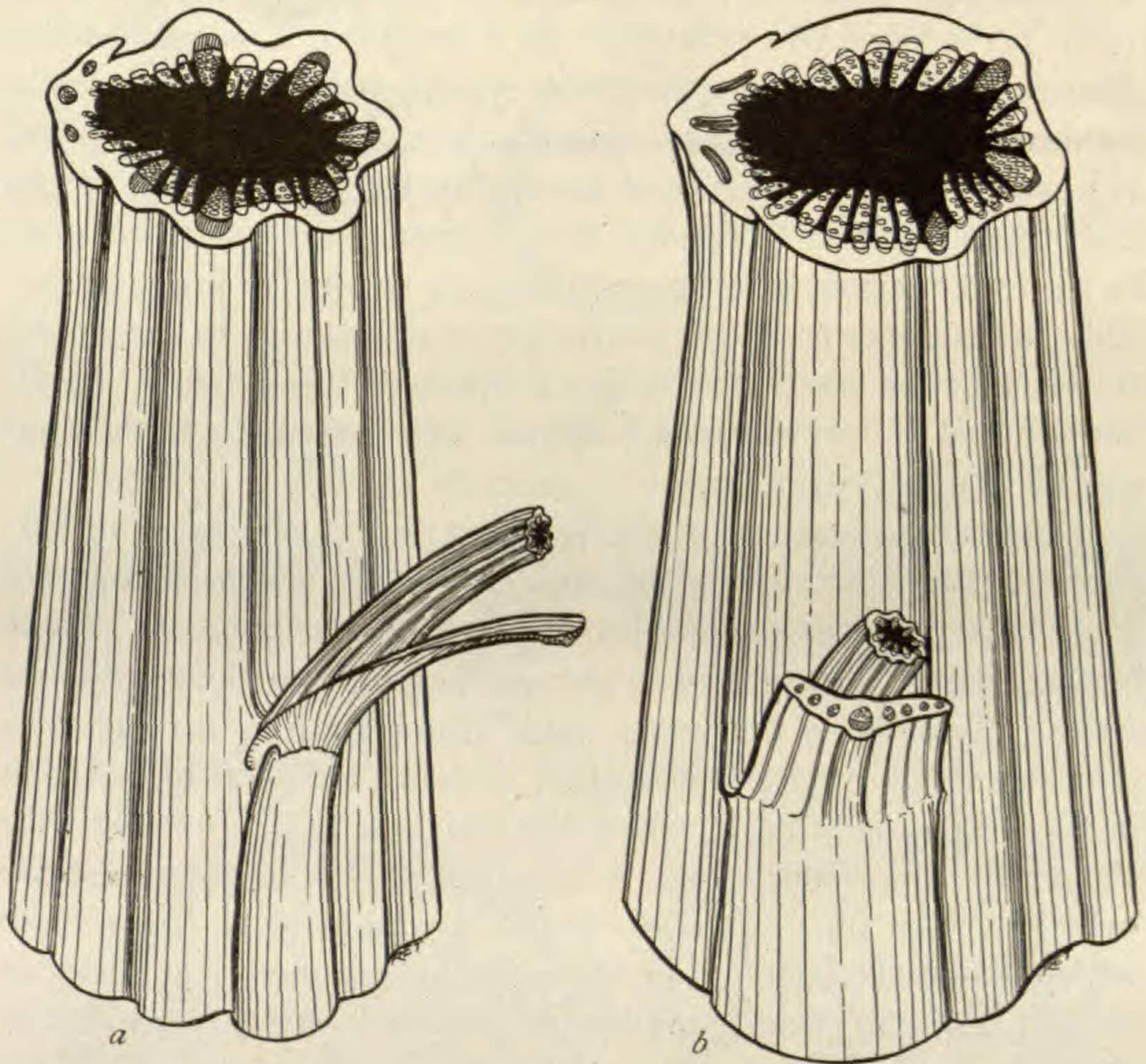


FIG. 3

Attention has already been given to the distribution of cambial activities in the nodal regions of herbaceous Dicotyledons. Another important factor in the development of the herbaceous type is shown in text fig. 3, which represents diagrammatically the stems of *Helianthus annuus* and *H. orgyalis*. In the former more herbaceous species a leaf base is represented on the left, at the upper end of the figure. This has 3 traces, as is normally the case in the genus. In addition to the 3 traces entering at the node, from the

leaf base are 6 others, emphasized in the diagram by the radial hatching of their outer regions. It is obvious that the traces of 3 leaves can be seen simultaneously in transverse sections of the stem. In other words, the leaf traces, together with their accompanying leaf rays, by their much elongated downward extension constitute an important topographical feature of the stem in many herbaceous Dicotyledons. In *b* is shown a corresponding diagram for *H. orgyalis*, a perennial species and one less typically herbaceous than *H. annuus*. Here only the traces of one other leaf can be seen. A feature of interest in the development of the herbaceous habit in *Helianthus* is the arrangement of the leaves. In the lower regions of intermediate types the leaves are opposite, while in the upper nodes the phyllotaxy is alternate. In the woody *H. hirsutus* the phyllotaxy is often opposite throughout. In *H. annuus* and *H. argyrophyllus*, annual and extremely herbaceous species, the leaf arrangement is generally entirely alternate.

Outstanding features of the organization of the extreme herbaceous type illustrated by the Monocotyledons are the occurrence of medullary strands and amphivasal fibrovascular bundles. These features are likewise present in extreme herbs in the dicotyledonous series. Text fig. 4 illustrates these characteristics for the two divisions of the Angiosperms. In *a* is shown the stem of *Sanicula* in the region of the node, where the leaf base is just uniting with the axis. An axillary bud is represented by its fibrovascular cylinder. The inner bundles of this are uniting by their faces with the opposite bundles of the main axis in such a manner as to give rise to typical amphivasal strands. These are clearly shown in *b*, which represents a lower plane of section than *a*. On the upper side of the cylinder are a number of amphivasal strands resulting from fusions between the bundles of axis and branch. In *c* the amphivasal strands have become collateral once more and the numerous foliar traces are seen entering the stem. In *d* is shown the nodal region of *Rumex* sp. The same method of formation of amphivasal strands is seen as in *Sanicula*, namely, by fusions between opposed strands of axis and branch. In this case the concentric bundles are so numerous as to be brought into the medullary region. In *e* is represented a lower plane of section

with a greater number of amphivasal bundles. In *f* the strands in the pith have reached their maximum number and are beginning to undergo fusions with the bundles of the wall of the cylinder.

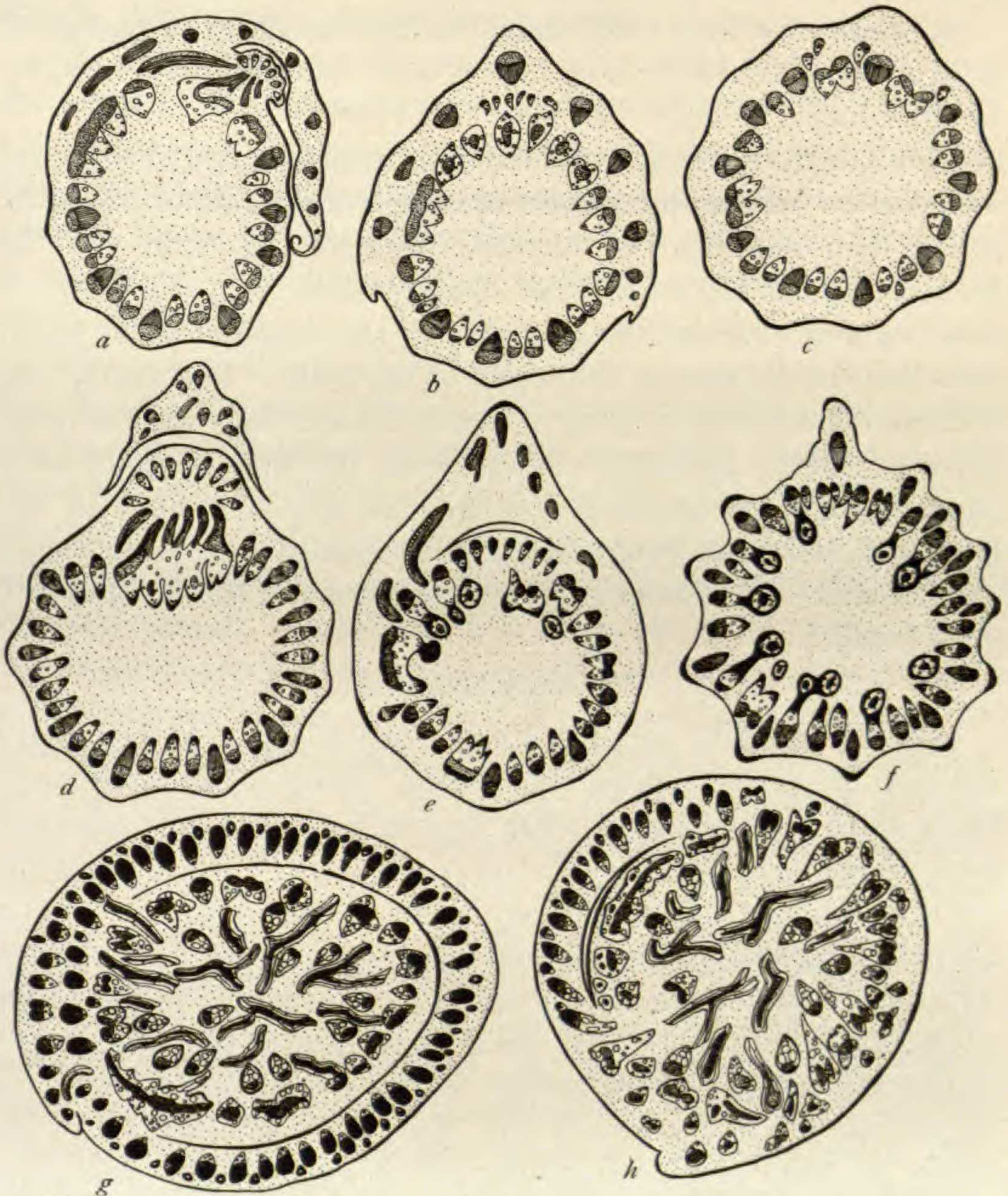


FIG. 4

The foliar traces are very numerous here as in *Sanicula*. In *g* and *h* are represented nodal sections of *Zea*. In *h* the leaf base has just fused with the axis and shows a very large number of bundles. In the central region of the stem many horizontal and vertical

unions of bundles are taking place, with the initiation of some amphivasal strands. In *h* the fibrovascular union of leaf and axis has advanced still farther, and many amphivasal bundles are present in the stem as a consequence.

It seems clear from these examples that the entry of numerous foliar strands at the node is correlated with the formation of amphivasal medullary strands. In most Dicotyledons these strands are the result of the facial fusion of the bundles of axis and branch, but such fusions are usually associated with a large number of foliar traces simultaneously entering the stem at the node. In the Monocotyledons the amphivasal strands result from the fusion of stem bundles with one another, or from the fusion of foliar traces with those of the stem in the region of the node. The amphivasal strand so characteristic of many higher Dicotyledons and the lower Monocotyledons probably originated in the first instance as a consequence of the fusions of stem bundles with stem bundles, and later, with the still further multiplied number of foliar traces characteristic of the Monocotyledons, by fusions of leaf bundles with stem bundles.

Conclusions

The various data introduced in this paper appear to justify the drawing of certain general conclusions. First of all, statements made as to the absence of foliar rays in herbs are not consistent with the facts of anatomy. Such rays are so characteristic a feature of organization of the more woody region of the aerial axis of herbs that they constitute a well marked diagnostic feature of such forms. The foliar rays of herbs are the result of the aggregation and fusion of the ordinary rays of woody stems, in relation to the foliar traces. Accompanying and characteristic of the process of fusion is the transformation of the vessels into fibers and the septation of the latter in turn into parenchymatous elements. The final consequence of this activity is the formation of large masses of storage tissue in relation to the incoming foliar traces. By comparison of nearly related species of the same genus, which are progressively more herbaceous, the following interesting conditions can often be observed. The accentuation of the herbaceous habit is accompanied by marked increase in the size of the leaf trace and of the

foliar ray to which it is related. Further, the foliar ray becomes much more homogeneously parenchymatous in more advanced and herbaceous species, and does not contain the admixture of vascular and fibrous elements which reveal the mode of origin of the foliar rays in more woody and primitive species.

The foliar ray surrounding and subtending the leaf trace is characteristic of the less advanced dicotyledonous herbs and of the lower more woody region of those higher in the herbaceous sequence. This type of ray gives place, by the later thinning of the woody cylinder, to one in which the storage tissue is confined to the flanks of the traces. The long vertical extension of these flanking rays results in the division of the originally continuous woody cylinder of the ancestral Dicotyledons into a circle of separate strands, the fibrovascular bundles. Of the strands thus resulting, those more closely related to leaves manifest an interesting contrast to the others because they very frequently manifest an absence of cambial activity. This cambial inactivity seems to be a safeguard against the undue consumption of assimilates in the growth in thickness of the foliar strands. Such growth in thickness would clearly not be advantageous to organisms dependent for their success in the struggle for existence on the amount of food stored up either in their stems or their seeds. The correctness of this interpretation of the undoubted fact that foliar traces lose or tend to lose their cambial activity in the stem of herbaceous Dicotyledons is vouched for by conditions observed in roots, to be enlarged upon in another connection. Roots permanently and perennially provided with root hairs are usually without secondary activity in the woody cylinder, while roots of allied species without persistent root hairs have the secondary tissues well developed. In other words, the more efficiently absorptive roots are without secondary growth, while roots of allied woody and less efficient species are well provided in this respect. In advanced herbs, such as the members of *Ranunculus*, the traces of leaves and roots stand out conspicuously in the subterranean stem by the absence of the secondary growth characteristically present in the fibrovascular strands of the stem proper.

It appears clear from these considerations that the herbaceous type is the extreme expression of efficiency, and that the correlated

reduction in or complete loss of secondary growth is physiologically advantageous to the plant.

An incidental and probably less essential modification in extreme herbs is the concurrence of medullary and amphivasal strands. These are apparently the result of the entry of very numerous bundles at the nodes, a feature of many advanced and angiospermous herbs. The resulting difficulties of accommodation are most readily overcome by the scattering and fusion of the crowded strands. In lower types the amphivasal and medullary bundles are the consequence of the fusion of facing cauline bundles of axis and lateral branch. In the highest herbs the foliar traces are concerned in the formation of medullary strands and in the scattered distribution of bundles throughout the transverse sections of the stem.

Summary

1. Herbaceous Dicotyledons have developed from arboreal dicotyledonous types by the formation of storage rays about the leaf traces.

2. In the more primitive herbs the foliar rays are shallow longitudinally, but of considerable radial depth.

3. In higher herbaceous Dicotyledons the foliar rays lose in radial dimensions as a result of the thinning of the woody cylinder, but this loss is largely compensated for by their increasing vertical extension, which often carries them through several internodes.

4. In the higher herbaceous Dicotyledons the foliar traces tend to multiply in number with the increased efficiency of the leaf.

5. Another important development in advanced dicotyledonous herbs is the progressive disappearance of cambial activity in the foliar trace, which often, in spite of this, is larger in size than the bundles of the stem.

6. The increase in number and importance of the foliar traces, as well as the greater relative importance of secondary axes in high herbs, leads to the crowding of strands at the node, which in turn results on the one hand in scattered distribution of the bundles in the stem, and on the other to formation of amphivasal strands.

7. The disappearance of secondary growth in foliar traces of advanced dicotyledonous herbs appears to be explainable on the grounds of physiological advantage.

8. Absence of secondary growth extends from the leaf traces to the rest of the bundles situated in the stem, and a condition practically monocotyledonous results.

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EXPLANATION OF PLATES I-VII

PLATE I

FIG. 1.—Transverse section of lower region of aerial stem of *Aster novae-angliae*, slightly magnified to show presence of foliar rays on upper left hand.

FIG. 2.—Transverse section of extreme upper slender portion of stem of *Aster novae-angliae*, slightly magnified to show alternation of leaf traces and leaf rays with ordinary stem bundles (approximately 8 of each).

FIG. 3.—Part of fig. 2, more highly magnified.

FIG. 4.—Part of fig. 2, more highly magnified.

FIG. 5.—Part of fig. 2, more highly magnified.

FIG. 6.—Leaf trace and subtending and flanking storage tissue, from slender upper portion of stem of *Aster novae-angliae*.

FIG. 7.—Leaf ray of *Helianthus annuus* in transverse section, slightly magnified.

PLATE II

FIG. 8.—Transverse section of foliar ray of *Helianthus orgyalis*, moderately magnified.

FIG. 9.—Longitudinal section of foliar ray of *H. tuberosus*, somewhat highly magnified to show mixed organization consisting of rays, fibers, and vessels.

FIG. 10.—Tangential section of leaf ray of *H. hirsutus*, showing it as yet incompletely aggregated from elements of ordinary wood and consequently consisting of an obviously mixed assemblage of wood rays, vessels, and fibers.

FIG. 11.—Tangential section of foliar ray of *H. tuberosus*, showing more advanced condition of foliar ray in more advanced herb; ray is broader, leaf trace larger, and structure more homogeneous than in fig. 10, which has same degree of magnification.

FIG. 12.—Foliar ray of *H. annuus*, very marked herbaceous species of the genus; magnification same as in two preceding figures, and shows that leaf trace is much larger, as is also the accompanying ray, which is further marked by a much greater advance toward homogeneity than two foregoing figures.

FIG. 13.—Part of fig. 12, more highly magnified to show presence of some degree of variety in elements composing foliar ray; magnification same as fig. 9, of *Helianthus tuberosus*.

FIG. 14.—Magnified view of part of fig. 10, representing ray of *H. hirsutus*; for purposes of comparison magnification is identical with figs. 9 and 13.

PLATE III

FIG. 15.—Transverse section of one of angles of upper region of aerial stem of *Helianthus tuberosus*, showing leaf trace in center flanked by stem bundles on either hand.

FIG. 16.—Right hand stem bundle of last figure, more highly magnified to show presence of cambial activity between xylem and phloem.

FIG. 17.—Transverse section of leaf trace in fig. 15, more highly magnified to show absence of cambial activity in foliar strand.

FIG. 18.—Transverse section of mature root of *Aster Shortii*, showing pentarchous organization with well developed secondary growth; root hairs have disappeared.

FIG. 19.—Transverse section of younger root of *A. Shortii*, about phase when secondary growth is beginning; root hairs still present but beginning to wither away.

FIG. 20.—Transverse section of persistently hairy root of *Aster umbellatus*; continued presence of root hairs correlated with absence of secondary growth.

PLATE IV

FIG. 21.—Transverse section of very herbaceous species of *Aster*, *A. tataricus*; normal woody structure of *Aster* replaced by herbaceous texture and by more foliar traces (7) than those usually present in species of the genus (3).

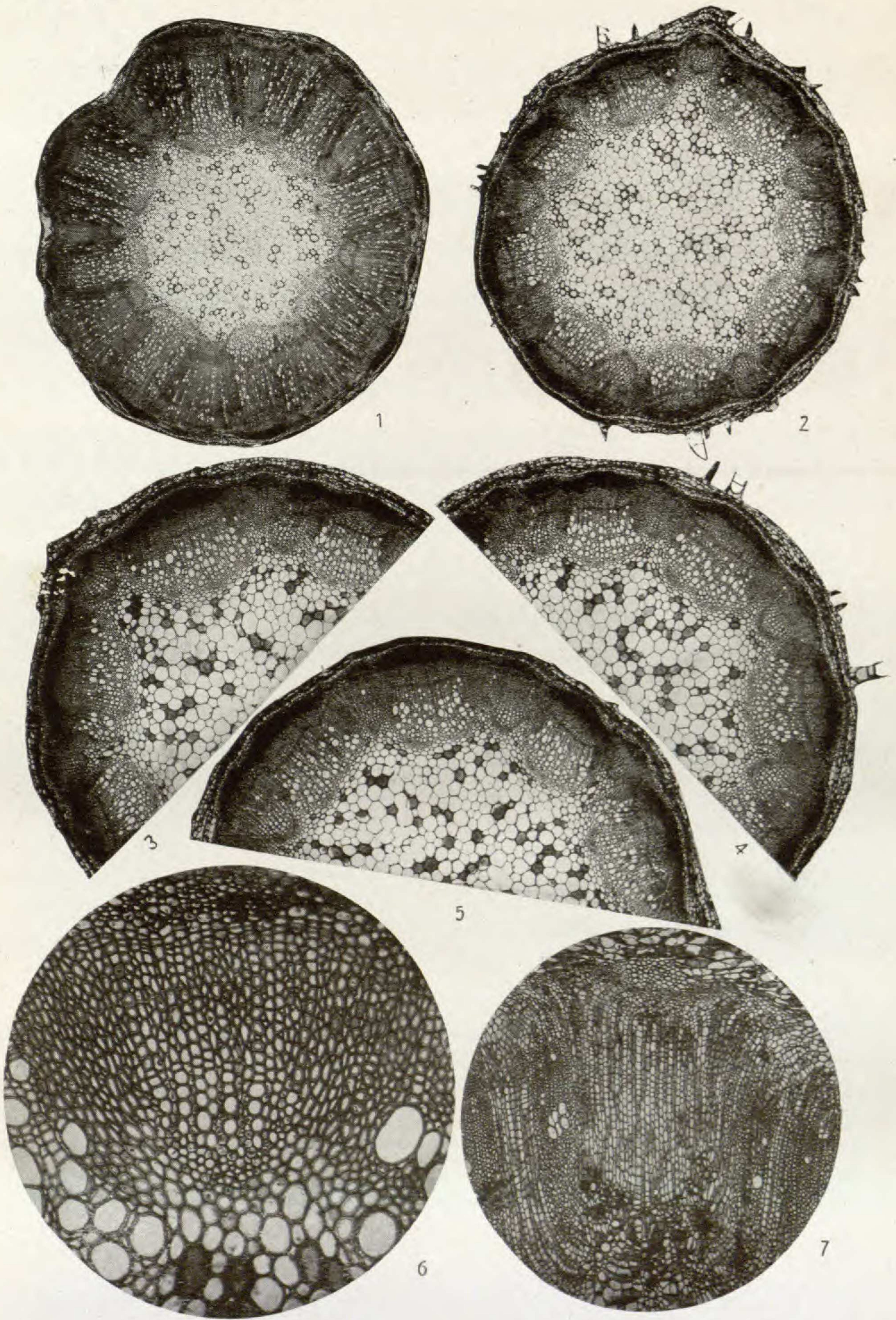
FIG. 22.—Transverse section of small branching stem of *Ranunculus acris*.

FIG. 23.—Transverse section of nodal region of larger branching stem of *R. acris*.

FIG. 24.—Transverse section of stem of *R. acris*, below node; 5 foliar traces in axis appear darker than stem bundles by reason of their vessels being occupied by gummosis.

FIG. 25.—Part of section similar to that shown in fig. 24, more highly magnified to show characteristic difference between foliar and cauline bundles.

FIG. 26.—Another of the same, showing different bundles.



JEFFREY and TORREY on ANGIOSPERMS